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Community structure of the intertidal meiofauna along a gradient of morphodynamic sandy beach types in southern Chile

Estructura comunitaria de la meiofauna intermareal en un gradiente de tipos morfodinámicos de playas arenosas en el sur de Chile

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ABSTRACT

Three sandy beaches located in southern Chile (Gaviotas, Guabún and Mar Brava; ca. 42° S) were studied during the summer of 2000 to analyse the patterns in abundance and biomass of the meiofauna along a gradient of morphodynamic beach types. Sediment samples were collected with metallic cylinders (23 cm^2 cross sectional area, 120 cm long) at ten equally spaced tidal levels along six transects separated between 5 and 10 m and extending from above the drift line down to the low tide level. Porosity, shear strength, water content, penetrability and grain size of the substrate were measured in each sampling level. The meiofauna was primarily represented by Nematoda and Copepoda Harpacticoidea. The highest average density and biomass per unit of area were found at the reflective beach of Gaviotas (6,172 ind 10 cm^{-2} and 2.38 g m^{-2}, ash free dry weight) as compared with the intermediate beach of Guabún (3,390 ind 10 cm^{-2} and 1.70 g m^{-2}) and the dissipative beach of Mar Brava (3,667 ind 10 cm^{-2} and 0.86 g m^{-2}). Total abundance and biomass of the meiofauna per linear meter of beach (i.e., total meiofauna in an intertidal across-shore transect 1 m wide) were higher at Mar Brava (506 x 10^6 ind m^{-1} and 119.4 g m^{-1}), as compared with Gaviotas (271 x 10^6 ind m^{-1} and 101.7 g m^{-1}) and Guabún (143 x 10^6 ind m^{-1} and 73.9 g m^{-1}). Therefore, these last results show a trend of increasing intertidal meiofaunal abundances and biomass towards the dissipative stage of the beach gradient analyzed. The highest meiofaunal densities and biomass occurred at the upper and mid shore levels of each beach. Lower across-shore variability in density and biomass were found at the dissipative beach. Results of a Monte Carlo permutation test showed that water content, penetrability and grain size were the best predictor variables of meiofaunal density. Body sizes of nematodes, copepods, turbellarians, halacarids and ostracods were correlated with sediment characteristics. In general, the relationship between community structure of the meiofauna and beach morphodynamics, were similar to that found for the macroinfauna from different sandy beaches around the world, suggesting that meiofauna and macroinfauna are similarly affected by the physical processes associated to different beach types.

Key words: sandy beach meiofauna, southern Chile.

RESUMEN

Se estudiaron tres playas arenosas del sur de Chile (Gaviotas, Guabún y Mar Brava; ca. 42° S) durante el verano del 2000 para analizar los patrones de abundancia y biomasa de la meiofauna a lo largo de un gradiente de tipos morfodinámicos de playas. Se recolectaron muestras de sedimento con cilindros metálicos (23 cm^2 de área, 120 cm de longitud) en diez niveles espaciados a intervalos regulares a lo largo de seis transectos separados de 5 a 10 m y extendidos desde un punto sobre el nivel de marea alta y el nivel de marea baja. En cada nivel de muestreo se midió porosidad, fuerza de cizalla, contenido de agua, penetrabilidad y tamaño del grano. La meiofauna estuvo primariamente representada por Nematoda y Copepoda Harpacticoidea. Las mayores densidades y biomasas medias por unidad de área se encontraron en la playa reflectiva de Gaviotas (6.172 ind 10 cm^{-2} y 2,38 g m^{-2}, peso seco libre de cenizas) en comparación con la playa intermedia de Guabún (3.390 ind 10 cm^{-2} y 1,70 g m^{-2}) y la playa disipativa de Mar Brava (3.667 ind 10 cm^{-2} y 0,86 g m^{-2}). La abundancia y biomasa total de la meiofauna por metro lineal de playa (i.e., meiofauna total contenida en un transecto intermareal de 1 m de ancho) fueron mayores en Mar Brava (506 x 10^6 ind m^{-1} y 119,4 g m^{-1}) versus Gaviotas (271 x 10^6 ind m^{-1} y 101,7 g m^{-1}) y Guabún (143 x 10^6 ind m^{-1} y 73,9 g m^{-1}). Por lo tanto, estos últimos resultados muestran una tendencia de aumento de abundancia y biomasa de la meiofauna intermareal hacia el tipo disipativo dentro del gradiente estudiado de tipos de playas. Los valores más altos de densidad y biomasa de la meiofauna se encontraron en los niveles superiores y medio de cada playa. En la playa disipativa, se encontró la menor variabilidad en abundancia y biomasa de la meiofauna a lo ancho del intermareal. Según la prueba de permutación de Monte Carlo, el contenido de agua, penetrabilidad y tamaño del grano fueron las variables que mejor predicen la variabilidad de las densidades de la meiofauna. Los tamaños corporales de nemátodos, copépodos, turbelarios, halacáridos y ostrácodos estuvieron correlacionados con las características del sedimento. En general, las relaciones entre estructura comunitaria de la meiofauna y morfodinámica de playas, fueron similares a aquellas encontradas para la macroinfauna de diferentes playas arenosas alrededor del mundo, lo que sugiere que la meiofauna y macroinfauna son afectadas similarmente por los procesos físicos asociados a diferentes tipos de playas.

Palabras clave: meiofauna de playas arenosas, sur de Chile.

INTRODUCTION

The intertidal sediments of exposed sandy beaches harbour a diverse and abundant meiofauna and macroinfauna (Brown & McLachlan 1990). Nematoda, Harpacticoidea, Turbellaria and Oligochaeta stand among the most common meiofaunal taxa (McLachlan 1988), while Crustacea, Polychaeta and Bivalvia are the most frequent macroinfaunal taxa (Brown & McLachlan 1990). Although several studies have analysed the responses of macroinfauna and meiofauna to single sediment characteristics, such as mean grain size and sorting of particles (see reviews by McLachlan 1983 and Coull 1988), composite abiotic indexes created to characterize morphodynamic beach states were not used until the 90's. The pioneer studies of McLachlan (1990) and McLachlan et al. (1993) related community structure of the intertidal macroinfauna to morphodynamic beach types (sensu Short & Wright 1983), showing that species richness, as well as, total abundance and biomass of the macroinfauna tended to increase from narrow beaches having coarse sands and steep slopes (reflective beaches, sensu Short & Wright 1983), to wider beaches having finer sands and flatter slopes (dissipative beaches, Short & Wright 1983). Similar studies have not been carried out with the sandy beach meiofauna, although McLachlan & Turner (1994) predicted that optimum conditions for the development of a diverse and abundant meiofauna are likely to occur in intermediate beaches. Their prediction was based upon the fact that beaches with intermediate morphodynamic characteristics represent an equilibrium state between organic inputs (which increases towards the dissipative beach state) and aerobic interstitial conditions (which increases towards the reflective beach state). Both factors are the most favorable to the presence on meiofauna in intertidal habitats (e.g., Giere 1993). To test this prediction, a number of beaches covering the full spectrum of morphodynamic beach states should be sampled.

The northern coast of Isla de Chiloé (southern Chile, circa 42° S) is ideal to examine the earlier prediction, since reflective, intermediate and dissipative beaches alternate in a reduced geographic area (Jaramillo et al. 2000). That allows to avoid eventual effects of confoundig factors which may vary geographically (e.g., sea water temperature, species replacement) along larger latitudinal gradients. While the sandy beach macroinfauna of this area of the the Chilean coast has been previously studied (Jaramillo et al. 2000), no meiofaunal studies have been conducted here or elsewhere along the wave exposed sandy beach of this coast. Since community structure and zonation of the intertidal meiofauna are highly affected by sediment (Hicks & Coull 1983, Giere 1993) and beach characteristics (McIntyre 1971, McLachlan 1980, McLachlan et al. 1981), it is reasonable to hypothesise that the community structure of the Chilean meiofauna is related to beach morphodynamics; i.e., it changes according to changes in physical characteristics occurring along a gradient of beach morphodynamic types (e.g., changes in grain sizes, porosity, water table depth). To provide a preliminary evaluation of this hypothesis and the prediction of McLachlan & Turner (1994) (i.e., higher densities and biomass of meiofauna in intermediate beaches), we sampled three morphodynamic beach types in the northern coast of Isla de Chiloé.

MATERIALS AND METHODS

Study area

The sites selected for sampling were at the central areas of the beaches of Guabún (41° 48' S, 74° 01' W) and Mar Brava (41° 54' S, 73° 59' W), located on the exposed coast of Isla de Chiloé (i.e., fully exposed to the Pacific Ocean, Fig. 1), and at the central area of the beach of Gaviotas (41° 51' S, 73° 45' W), located on the less exposed coast of Golfo de Ancud (Fig. 1). Tides in this region are semidiurnal with maximum tide ranges close to 2 m. A previous study characterised Gaviotas as a reflective beach, Guabún as intermediate and Mar Brava as dissipative (Jaramillo et al. 2000).

Meiofauna sampling

Samplings were carried out during spring tides of January 2000. Sediment samples were collected with metallic cylinders (23 cm^2 cross sectional area, 120 cm long) at ten equally spaced levels along six replicated transects (separated haphazardly between 5 and 10 m) and extending from above the drift line to the swash zone. The uppermost station was located above the drift line (level 10), the second at the drift line (level 9) and the last (level 1) at the lowest limit of the swash zone (indicated by bore collapse). Previous studies of vertical distribution of meiofauna in exposed beaches (e.g., McLachlan 1980) showed that the highest meiofaunal abundances are usually found in wet sands above the water table level; thus, for quantitative studies it is necessary to reach that level. Since water table depth increases up the beach, the sampling depth increased from lower

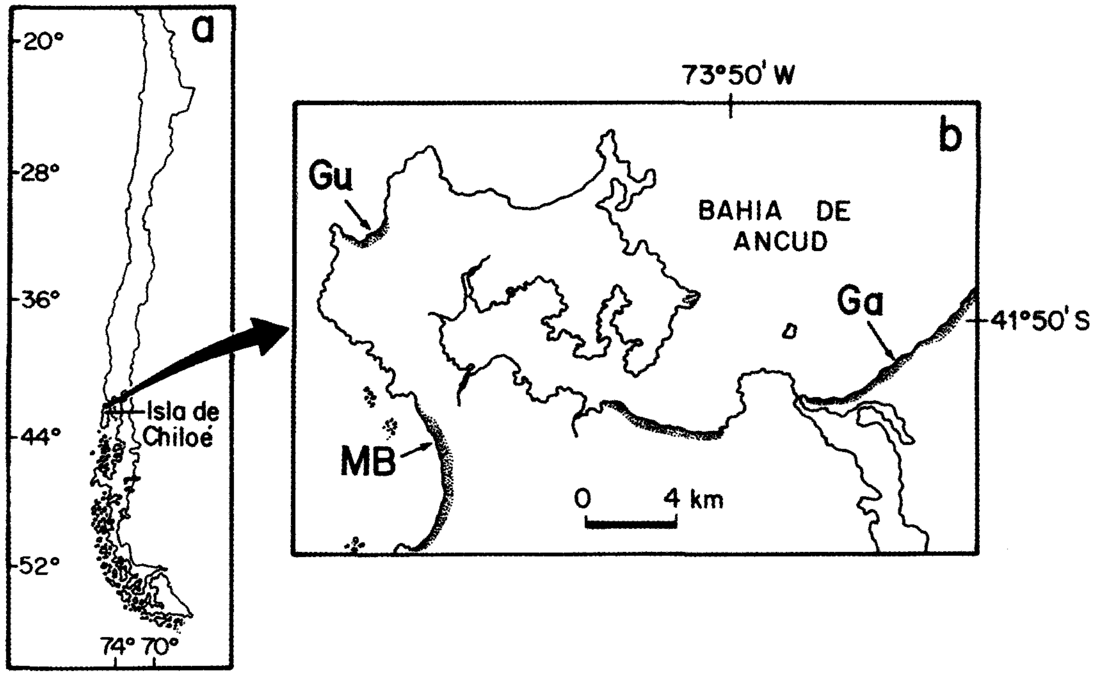

Fig. 1: Location of the sandy beaches studied at Isla de Chiloé, southern Chile.
Ubicación de las playas arenosas estudiadas en la Isla de Chiloé, sur de Chile.

to upper beach levels (i.e., from 40 to 120 cm). Each sediment sample was homogeneised by hand in a small plastic tube before collecting subsamples of 100 cm^3 and 40 cm^3 with plastic corers for meiofaunal and sedimentological analyses, respectively. Subsamples for meiofauna were kept in 250 cm^3 plastic jars with 40 cm^3 of seawater previously filtered through APFF Millipore glass microfibre filters. 40-100 µg of menthol were added to each jar as an anaesthetic. After 24 h, the samples were stored in formaldehyde 6 % with Rose Bengal and borax. To extract the meiofauna, water was added to each sample which was stirred and later on decanted for less than 10 seconds in a plastic graduated cylinder (6.4 cm in diameter, 33 cm length). After decantation, the supernatant was filtered through a 42 µm sieve (Pfannkuche & Thiel 1988). This procedure was repeated six times resulting in an extraction efficiency of about 97 % (efficiency estimated by examination at 40x of residual sediment of six samples ramdomly selected). Meiofaunal samples retained in the 42 µm sieve were separated through a set of sieves of different mesh sizes: 1,000, 500, 200, 100 and 42 µm. The meiofauna was sorted to major taxa using an inverted microscope (100 x) in a modified Bogorov zooplankton tray. Indirect estimates of biomass (ash free dry weights) were carried out by using the individual weights previously measured in meiofaunal taxa by McLachlan (1977b), Faubel (1982) and Widbom (1984). Abundance and biomass values per running meter of beach (i.e., estimates of total meiofauna in an intertidal across shore transect of 1 m wide) were obtained by linear interpolation between sampling stations, after obtaining mean values of biomass and abundances per m^2 at each sampling station. An indirect average size of the meiofauna was calculated for each major taxa by pondering mesh size of sieves with the relative abundances of organisms retained in each sieve (e.g., if 50 % of the organisms of a major taxa are retained in a mesh sieve of 100 µm mesh and 50 % are retained in a mesh sieve of 42, the estimated indirect average size is 71 µm).

Substrate characteristics

At each beach level, a superficial sampling (0-6.5 cm of depth) of sediment was taken along one of the central transects to determine porosity, water content and granulometry. Porosity and water content were estimated by gravimetric differences (Giere et al. 1988). Grain size of sands was analysed by using a Coulter LS 200 laser diffraction particle size analyser, while that of the coarser fraction by dry sieving (Folk 1980). Penetrability and shear strength were measured (n = 6) at the same beach levels where sediment samples were collected. Penetrability and shear strength were measured with a penetrometer and a shear vane meter. The penetrometer was a 120 g metal rod, 35 cm in length and 7.5 mm diameter, which was dropped from 1 m above ground level. The vane tester (English Drilling Equipment Co. Ltd., England) comprises a torque head with a direct reading scale which is turned by hand. A non - return pointer indicates the reading. The vane (33 mm diameter) which is screwed into the rear of the torque head was pushed 5 cm into the sediment (the same extension of the vane). The readings are given in kPa. The beach face slope at the site of the transects was analysed with Emery's profiling technique (Emery 1961).

Statistical analyses

Non-metric multidimensional scaling ordination (MDS) with the Bray-Curtis similarity measure and cluster analysis (Bray-Curtis index, group-average linkage) were performed on double square root transformed abundance of major taxa. Pairwise analysis of similarities (ANOSIM, Clarke 1993) was carried out to test the null-hypothesis that there were no differences (at $\alpha = 0.05$) in the composition of the meiofaunal assemblage at different beaches. MDS, cluster analysis and ANOSIM were performed using the software package PRIMER, developed at the Plymouth Marine Laboratory (Clarke & Warwick 1994). Redundancy analysis (RDA) was used to evaluate the relation between the average density of the meiofauna per tidal level and the environmental variables. RDA is the canonical form of principal component analysis, a form of direct gradient analysis (ter Braak 1995). Linearity between the abundances of the major taxa and the environmental gradients is assumed for RDA. Linearity was previously checked with biplots created with log (x + 1) transformed abundances of the major taxa vs. environmental variables (n = 30). The taxa which showed any cuadratic relation ('unimodal', sensu Ter Braak, 1995) with the environmental variables were not included in the RDA. To select the environmental variables which significantly explained the variability in the abundance of the meiofauna ($\alpha = 0.05$) a Monte Carlo permutation test was carried out. The variance explained by the RDA model was calculated as the sum of eigenvalues axes (Bocard et al. 1992). The RDA and the Monte Carlo permutation tests were carried out with CANOCO for Windows (ter Braak & Smilauer 1998). Spearman correlation analyses were carried out with SPSS for Windows to study the relation between average sizes of the major meiofaunal taxa and environmental variables. Only the taxa which showed high variability in average size were included in the analyses.

RESULTS

The physical environment

The beaches of Gaviotas and Guabún had similar intertidal widths and beach profiles, while Mar Brava (135 m) was about three times wider and four times flatter (Fig. 2). The substrate characteristics of the beaches are shown in Table 1. Sands from the reflective beach of Gaviotas corresponded to coarse and very coarse sands, that of the intermediate site at Guabún to medium sands, while that of the dissipative beach at Mar Brava corresponded to fine sands (sensu Folk 1980). In Gaviotas and Mar Brava, sands were coarser at the lower shore levels, while at Guabún

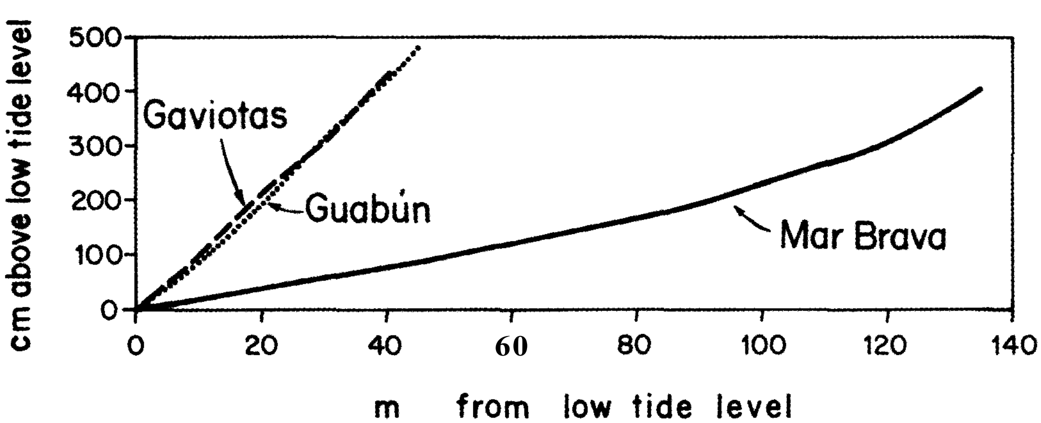

Fig. 2: Beach face slopes at the sites studied.
Perfiles de playa en los sitios estudiados.

TABLE 1

Physical characteristics at each zone of the beaches studied: D = dry zone, Rt = retention zone, Rs = resurgence zone, S = swash zone

Características físicas en cada una de las zonas de las playas estudiadas: D = zona de secado, Rt = zona de retención, Rs = zona de resurgencia, S = zona de batido de las olas

Beach	Zone	Porosity (%)	Water saturation (%)	Penetrability (kPa)	Shear strength (kPa)	Grain size (μm)	Sorting
Gaviotas	D	30.7	4.8	0.9	2.2	1152.0	3.0
	Rt	34.8	40.1	3.2	4.1	928.7	2.9
	Rs	30.0	95.1	2.9	4.0	1146.0	3.1
	S	33.0	95.0	1.9	2.0	2118.0	2.2
Gaubún	D	41.6	9.5	0.3	3.9	506.2	1.8
	Rt	41.4	41.5	1.6	8.3	452.7	1.9
	Rs	42.0	87.5	5.2	3.7	310.7	1.8
	S	40.3	96.7	3.2	3.3	313.8	1.6
Mar Brava	D	42.9	70.1	11.0	13.8	199.6	1.5
	Rt	38.0	100.0	11.4	8.9	204.2	1.4
	Rs	41.4	94.9	7.1	4.9	228.9	1.6
	S	36.5	100.0	6.3	3.7	227.5	1.6

the coarsest sands were found up shore (Table 1). The worst and best selected sediments were found at Gaviotas and Mar Brava, respectively. Porosity ranged between 30-35 % at Gaviotas and 40-42 % and 36-43 % at Guabún and Mar Brava, respectively (Table 1). Water saturation increased from the dry zone to the resurgence and swash zones at Gaviotas and Guabún, while it was quite homogeneous at Mar Brava. Penetrability and shear strength values indicate that the sediments of Mar Brava had a higher compaction than those of Gaviotas and Guabún (i.e., harder sands) (Table 1).

Composition and abundance of the meiofauna

Meiofauna was primarily represented by Nematoda and Copepoda Harpacticoidea. Crustacean nauplii, oligochaetes, halacarids, turbellarians, mystacocarids, ostracods, tardigrades, gastrotrichs, kinorhynchs and foraminiferans were also present but in lower abundances. Pre-zoea larvae and zoea of *Emerita* (at the two lowest levels of Gaviotas and Guabún), interstitial polychaetes, insects, syncarids (at the four lowest levels of Gaviotas) and interstitial isopods (at the lowest level of Gaviotas) were also found.

The number of major taxa was higher at the reflective beach of Gaviotas (15) and the intermediate site of Guabún (14), and lower at the dissipative beach of Mar Brava (6) (Table 2). Nematodes (64 %), harpacticoid copepods (14 %), crustacean nauplii (8 %) and halacarids (5 %) accounted for 91 % of abundance of the whole meiofauna at Gaviotas. Nematodes (41 %), harpacticoid copepods (20 %), oligochaetes (13 %), mystacocarids (8 %) and halacarids (4 %) accounted for 87 % of the meiofauna at Guabún, while nematodes (89 %), harpacticoid copepods (4 %), turbellarians (2.6 %) and gastrotrichs (2.6 %) accounted for 98 % of the meiofauna at Mar Brava.

The highest density and biomass of the meiofauna were found at the upper and mid shore levels of Gaviotas. Density and biomass values as high as 11,550-13,992 ind 10 cm^{-2} and 4.02-4.61 g m^{-2} were estimated for this beach (Table 3). The highest density and biomass estimated for the beaches of Guabún and Mar Brava were 7,110-9,900 ind 10 cm^{-2} and 3.76-4.10 g m^{-2} and 4,250-7,504 ind 10 cm^{-2} and 1.08-1.75 g m^{-2}, respectively (Table 3). The highest total abundance and biomass of the meiofauna per linear meter of beach (i.e., abundance and biomass of the meiofauna in an intertidal across-shore transect 1 m wide) were estimated for Mar Brava (506 x 10^6 ind m^{-1} and 119.4 g m^{-1}), as compared with Gaviotas (271 x 10^6 ind m^{-1} and 101.7 g m^{-1}) and Guabún (143 x 10^6 ind m^{-1} and 73.9 g m^{-1}) (Table 2).

Intertidal zonation of the meiofauna

The intertidal variability in total abundance and biomass of the meiofauna and the across shore

TABLE 2

Density (ind 10 cm^{-2}) and biomass (g m^{-2}) of the total meiofauna at the beaches studied

Densidad (ind 10 cm^{-2}) y biomasa (g m^{-2}) de la meiofauna total en las playas estudiadas

Shore level	Gaviotas (ind 10 cm^{-2})	Guabún (ind 10 cm^{-2})	Mar Brava (ind 10 cm^{-2})	Gaviotas (g m^{-2})	Guabún (g m^{-2})	Mar Brava (g m^{-2})
10 (uppermost level)	660	9,900	3,619	0,15	4,10	0,79
9	4,939	5,500	1,330	1,45	2,42	0,27
8	11,550	7,100	7,504	3,73	3,76	1,75
7	13,992	1,920	2,996	4,61	1,00	0,72
6	12,257	1,560	4,248	4,02	0,56	1,08
5	7,336	1,488	3,822	2,09	0,68	0,87
4	2,136	2,195	3,156	1,64	1,42	0,73
3	4,182	1,376	3,432	2,14	1,07	0,82
2	2,155	1,996	4,250	1,77	1,61	1,03
1 (lower level)	2,515	868	2,315	2,15	0,41	0,56
Mean	6,172	3,390	3,667	2,38	1,70	0,86

distribution of the major taxa is shown in Fig. 3. At Gaviotas, total abundance and biomass peaked at the sampling levels located at the retention zone (Fig. 3). At Guabún total abundance and biomass peaked at the drying zone and upper levels of the retention zone (Fig. 3). The total abundance and biomass showed less spatial variability at Mar Brava although slightly lower values were found at the upper shore levels (Fig. 3).

The density distribution of nematodes followed different patterns among the three beaches (Fig. 3). Nematodes at Gaviotas showed higher abundances at the retention and resurgence zone (3,900-10,600 ind 10 cm^{-2} versus densities of 55-372 ind 10 cm^{-2} in the swash zone). At Guabún, the density of this group was higher at the dry zone and the upper levels of retention zone, while at Mar Brava the intertidal distribution of nematodes did not show much spatial variability. While the harpacticoid copepods at Gaviotas showed low intertidal variability, they peaked at the dry zone and the upper levels of the retention zone at Guabún and at the dry and retention zones at Mar Brava (Fig. 3). At the latter, harpacticoid copepods were absent from the lowest shore levels (swash zone, Fig. 3).

The maximum number of nauplii larvae at Gaviotas occurred at the swash zone. At Guabún this group peaked significantly at the dry zone, while at Mar Brava they showed a fairly homogeneous distribution across the intertidal (Fig. 3). Foraminiferans were absent at the highest beach levels of the three beaches, specially at Mar Brava (Fig. 3). The intertidal distribution of turbellarians at Gaviotas showed maximum abundance values at the retention zone. At Guabún the maximum abundances of this group were found at the retention and swash zone, while at Mar Brava they showed a homogeneous distribution throughout most of the intertidal but the upper shore levels (dry zone) (Fig. 3).

Halacarids and ostracods were absent from the lower shore levels at Guabún; at this beach, ostracods peaked at the retention zone. The intertidal distribution of Gastrotricha was wider at Mar Brava; at Gaviotas and Guabún they were absent from the upper shore levels (Fig. 3). Interstitial polychaetes and oligochaetes showed opposite patterns of distribution; polychaetes were primarily found in the lower shore levels, oligochaetes were mostly found at the upper shore levels. While tardigrades primarily occupied the upper shore levels of Gaviotas and Guabún, they were not found at Mar Brava (Fig. 3).

TABLE 3

Number of major taxa, abundance and biomass of the total meiofauna per linear meter of beach at the sites studied

Número de taxa mayores, abundancia y biomasa de la meiofauna total por metro lineal de playa en los sitios estudiados

Beach	Number of major taxa	Abundance (106 ind m^{-1})	Biomass (g m^{-1})
Gaviotas	15	271	101.7
Guabún	14	143	73.9
Mar Brava	6	506	119.4

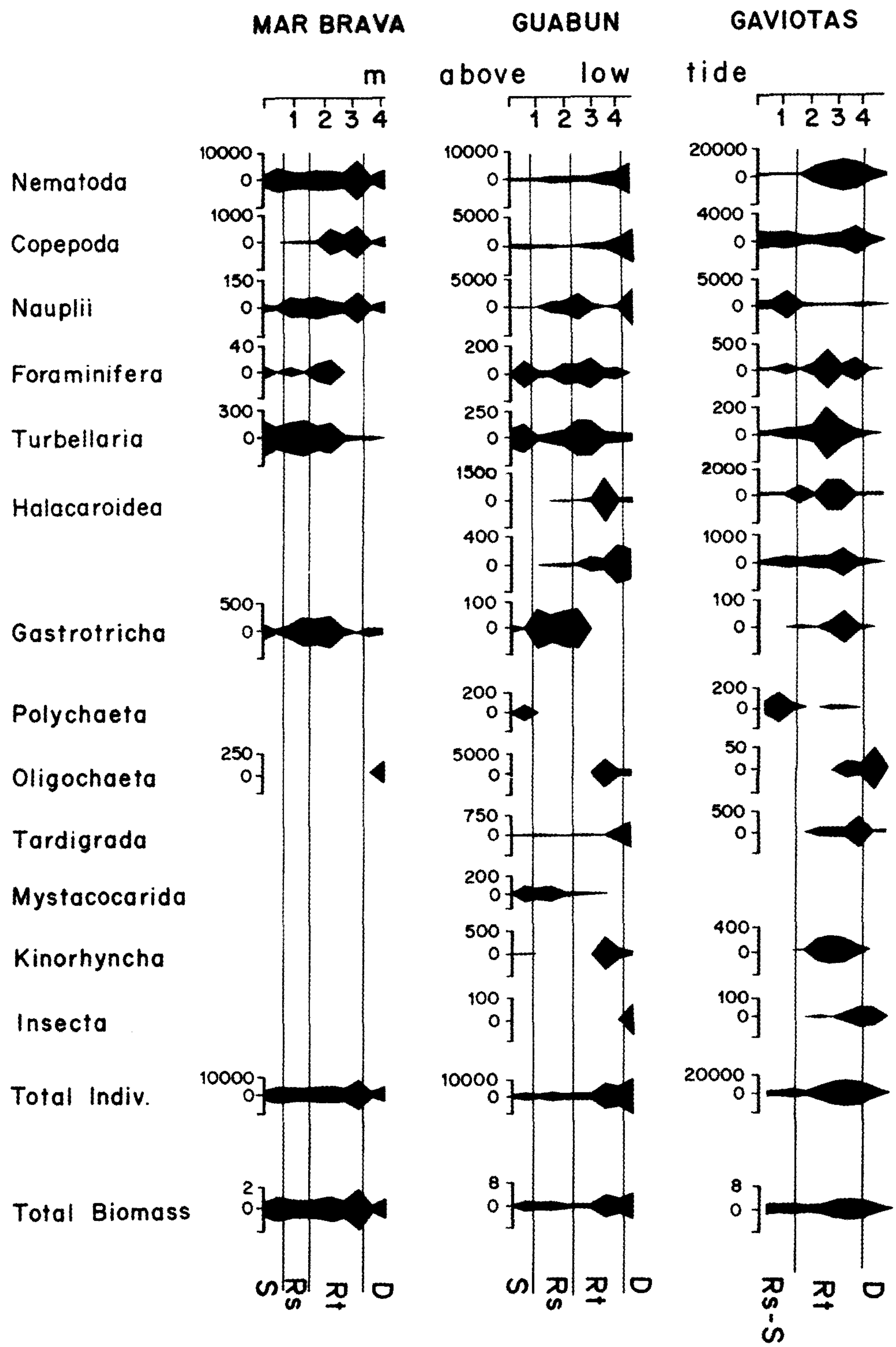

Fig. 3: Distribution of the major taxa of the meiofauna at the intertidal of Gaviotas, Guabún and Mar Brava. Density values are expressed in numbers 10 cm^{-2}, biomass in g m^{-2}. Dashed lines separate the physical zones of the beaches (sensu Salvat 1964): D = dry zone; Rt = retention zone; Rs = resurgence zone; S = swash zone.

Distribución de los taxa mayores de la meiofauna en el intermareal de Gaviotas, Guabún y Mar Brava. Los valores de densidad se expresan en número 10 cm^{-2}, los de biomasa en g m^{-2}. Las líneas discontinuas separan las zonas físicas de las playas (sensu Salvat 1964): D = zona de secado; Rt = zona de retención; Rs = zona de resurgencia; S = zona de batido.

Mystacocarids were only found at the lower shore of Guabún, while kinorhynchs and interstitial insects occurred only at Gaviotas and Guabún (Fig. 3).

Spatial patterns of the meiofauna

Figures 4 and 5 show the dendrogram and biplot resulting from the dendrogram and MDS analyses respectively. Meiofaunal assemblages from Guabún and Gaviotas were more similar between them (ANOSIM, R = 0.27) than between Guabún and Mar Brava (ANOSIM, R = 0.67) (higher R values indicate lower similarity, Legendre & Legendre 1998). Figures 4 and 5 suggest that Mar Brava was the beach with the lowest variation among sampling levels.

Relationships between meiofauna and environmental variables

Figure 6 shows the RDA ordination biplot obtained for the major taxa of meiofauna. The Monte Carlo permutation test showed that the meiofauna community changed significantly with grain size ($P < 0.001$), water saturation ($P < 0.05$) and sediment penetrability ($P < 0.001$). The total explained variation was 36.6 %. The first and second axis, explained by the environmental variables, accounted for the 93.5 % of the species-environment correlations. The sum of all canonical eigenvalues was 35.9 %.

The position of the meiofaunal groups in the biplot reflects the contribution of each group to the variance explained by the first two axes. Thus, the numbers of turbellarians and foraminiferans were not correlated with environmental variables since their positions in the RDA were near the origin (Fig. 6). The angles between variables in the biplot reflect their correlations (Legendre & Legendre 1998): angles near 90° indicate no correlations, angles near 0° indicate high positive correlation and angles near 180° indicate high negative correlation. Thus, the abundance of gastrotrichs was positively correlated with water saturation, while harpacticoid copepods and oligochaetes were negatively correlated with the same variable (Fig. 6). Copepods and nauplii larvae were positively correlated with grain size of sands, while the abundances of nematodes and gastrotrichs were negatively correlated with sand size (Fig. 6). Finally, the abundance of gastrotrichs was positively correlated with sediment penetrability; those of the harpacticoid copepods and oligochaetes were correlated negatively with the same variable (Fig. 6).

Average size of the meiofauna and environmental variables

Figure 7 shows the relations between indirect average size of the major meiofaunal taxa and the environmental variables. The average size of harpacticoid copepods and ostracods was negatively correlated with sediment porosity (r_s = -0.47 and -0.57, respectively; $P < 0.05$) and positively with grain size of sands ($r_s = 0.76$, $P < 0.001$ and $r_s = 0.69$, $P < 0.01$ for copepods and ostracods, respectively). Size of harpacticoid

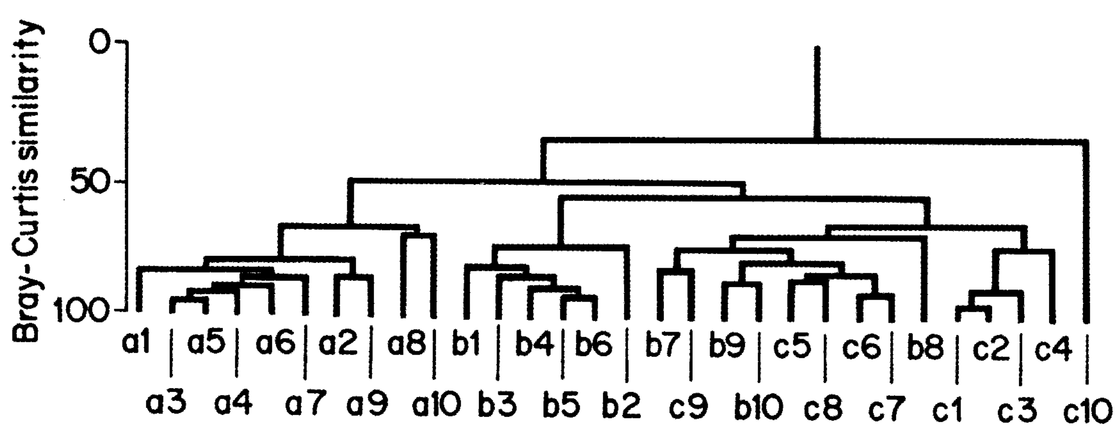

Fig. 4: Dendrogram resulting from hierarchical cluster analyses of the meiofauna. Lower case letters indicate beaches while numbers represent sampling levels: a = Mar Brava; b = Guabún; c = Gaviotas.

Dendrograma resultante del análisis de conglomerados jerárquico de la meiofauna. Las letras minúsculas indican playas mientras que los números representan los niveles de muestreo: a = Mar Brava; b = Guabún; c = Gaviotas.

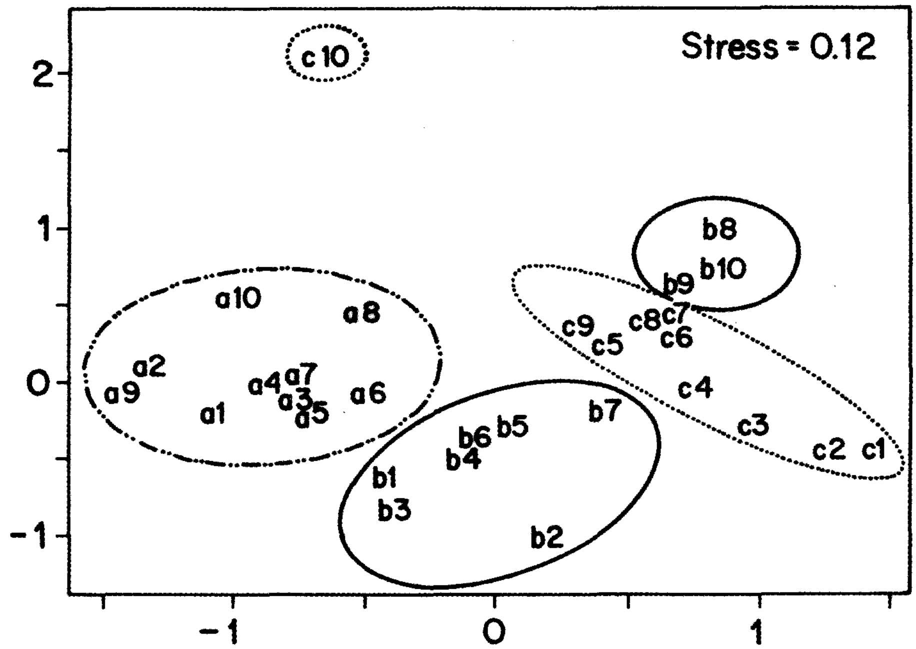

Fig. 5: Biplot resulting from the multidimensional scaling analyses of the meiofauna. Lowe case letters indicate beaches while numbers represent sampling levels (see Fig. 4).

Biplot resultante del análisis de escalamiento multidimensional de la meiofauna. Las letras minúsculas indican playas mientras que los números representan los niveles de muestreo (ver Fig. 4).

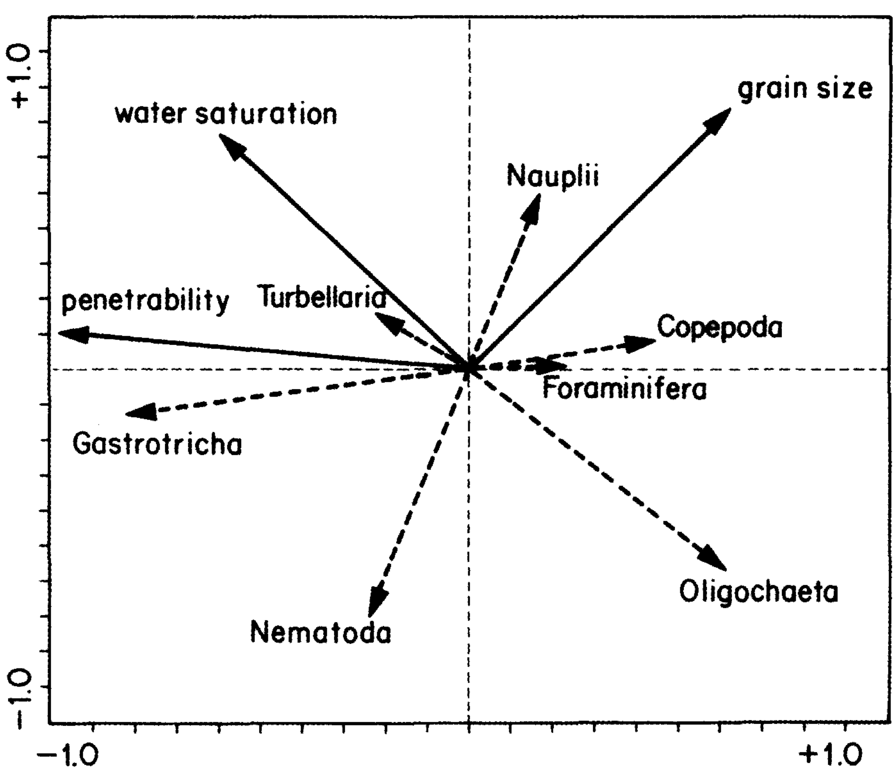

Fig. 6: Biplot resulting from the redundancy analyses. Dashed arrows for the major taxa, full-line arrows for the environmental variables. The arrows indicate the direction of increase for the variables studied.

Biplot resultante del análisis de redundancia. Flechas con líneas discontinuas para los taxa mayores, flechas con líneas continuas para las variables ambientales. Las flechas indican la dirección de aumento para las variables estudiadas.

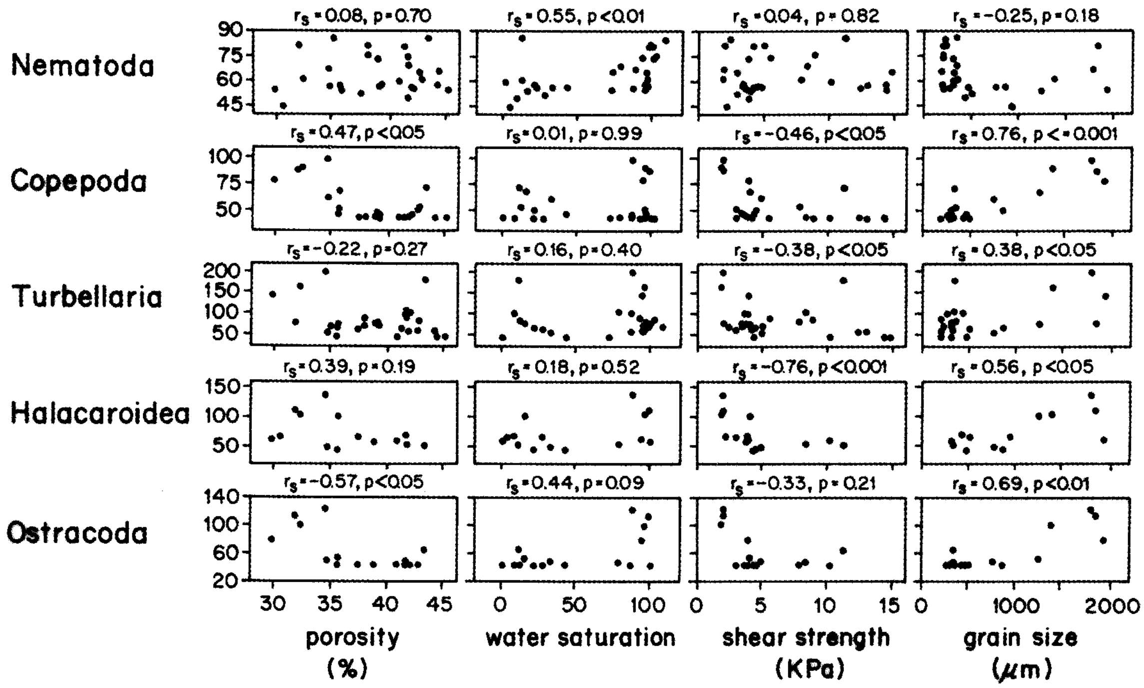

Fig. 7: Biplots of the indirect average size of the major groups of the meiofauna versus the environmental variables.

Biplots del tamaño medio indirecto de los taxa mayores de la meiofauna versus variables ambientales.

copepods was also negatively correlated with shear strength ($r_s = -0.46$, $P < 0.05$). That of nematodes showed significant positive correlation with water saturation ($r_s = 0.55$, $P < 0.01$).

DISCUSSION

The results of this study show that the highest density and biomass values per unit area of the total meiofauna occurred at the reflective beach of Gaviotas, as compared to the intermediate and dissipative sites. However, and due to the fact that the beaches studied differed in the width of the sampling zone, interbeach comparisons of density values can be misleading since across shore distribution of the meiofauna is not accounted for. The following figures exemplify this: two beaches of similar length but different intertidal width (e.g., 100 versus 200 m) may have the same density of meiofauna per square meter. However, the wider beach will have twice the intertidal density. Thus, comparisons based on linear meter of beach sampled (i.e., estimations on an intertidal transect of 1-m wide) allow to truly know which beach harbours higher densities in its intertidal area. The comparative analyses of this study showed that abundance and biomass of the total meiofauna per linear meter of beach were higher towards the dissipative side of the beach spectrum analyzed. This trend is similar to that usually found for the sandy beach macroinfauna; i.e., abundance and biomass per linear meter of across shore intertidal increase from reflective to dissipative beaches (McLachlan et al. 1993, 1996, 1998). On the other hand, the trend shown by richness of major meiofaunal taxa was the opposite to that shown by the macroinfauna elsewhere. Thus, while species richness of the sandy beach macroinfauna increases from reflective to dissipative sites (McLachlan et al. 1993, 1996, 1998), richness of major meiofaunal taxa decreased along this gradient. But this pattern should be taken with caution since in this study we only analysed richness of major taxa, and species richness could still show a different trend. It is possible to suggest that higher density and biomass values (in units per area or ind m^{-2}), as well as higher number of major meiofaunal taxa at the reflective and intermediate beaches of Gaviotas and Guabún are related to these beaches having coarser sand grains than the dissipative beach of Mar Brava, and consequently the interstitial habitat at the former beaches are more flushed and oxygenated (cf. McLachlan 1988). As shown by some authors (Giere 1993, Berninger & Epstein 1995, Moodley et al. 1997), the concentration of interstitial oxygen is one of the most relevant physical factors affecting presence of meiofauna in intertidal habitats.

Other studies have reported meiofaunal densities between 4 and 11,820 ind 10 cm^{-2} (McIntyre 1969, Coull 1988), although most values for sandy beaches lie between 50 and 1,500 ind 10 cm^{-2} (McIntyre 1969). Thus, while the densities estimated in this study (3,390-6,171 ind 10 cm^{-2}) can be considered high, the biomass values (0.86-2.38 g m^{-2}) fit well within the biomass figures reported for the intertidal of exposed beaches, i.e., 0.020-4.4 g m^{-2} on other coasts of the world (McLachlan 1983). It was also found that nematodes and harpacticoid copepods were the most abundant taxa, which is typical in all kinds of sediments (Coull & Bell 1979, Coull 1988).

The intertidal distribution of the total meiofauna at Gaviotas and Guabún was noticeably compressed downshore as compared with that at Mar Brava (Fig. 3). McLachlan (1983) mentions that in exposed sandy beaches the zone of resurgence is the most suited for interstitial life, since there is a good balance among water content, oxygen and food supply and physical stability. Giere (1993) has mentioned that in exposed sandy beaches, the swash zone is characterised by an impoverished meiofauna. Similar compressed patterns of downshore distribution have been found at exposed beaches on the Pacific coast of USA (Wieser 1959), east coast of India (Ganapati & Rao 1962, McIntyre 1968) and east coast of South Africa (McLachlan 1977b). The intertidal distribution of the numbers of the meiofauna at Mar Brava was the most uniform, as that found in other dissipative and/or relatively protected beaches (cf. Harris 1972, McLachlan 1977b). The fact that at Mar Brava the zonation was more uniform might well be related to the lower variability of physical intertidal characteristics, specially water saturation (see Table 1).

Even when the three beaches studied are morphodynamically different, the zonation of the major taxa of meiofauna was quite similar at Gaviotas and Guabún (Fig. 3). Although the size of sand grains was quite different between these beaches, the beach face slope and water saturation were very similar. This suggests that the zonation of the intertidal meiofauna of exposed sandy beaches may be related to a combination of physical factors (such as the morphodynamic beach stage, sensu Short & Wright 1983) rather than to single ones, such as grain size. This would explain the low percentage (36 %) of the meiofaunal variability explained by the three physical variables included in the redundancy analysis.

Results presented in Fig. 3 show that the three beaches differ in the composition of their meiofauna, and mainly in the relative proportion of nematodes and crustaceans. This fact fits well with the hypothesis that the nematode/copepode ratio is negatively correlated with grain size in non-polluted sediments (Warwick 1981). McLachlan (1977a) found an increase in the proportion of crustacean with an increase in wave exposure. Thus, the relationship between nematodes and crustaceans could be an indicator of the energetic and morphodynamic conditions of exposed sandy beaches.

Sediment characteristics have a dominant role in meiobenthic ecology (Giere 1993). Indeed, grain size determines many physiographic parameters which are closely related to substrate such as porosity, permeability and oxygen supply (Giere et al. 1988). Orren et al. (1981) and Hennig et al. (1983) found that the densities of nematodes and copepods were negatively correlated with grain size at exposed beaches of South Africa. In this study, the RDA showed correlations with nematodes, but not with copepods. This may be explained by the fact that the density of the copepods at the beaches studied was more influenced by sediment penetrability than by grain size.

Virtually all the meiofauna is interstitial (i.e., no burrowing) in sands coarser than 200 µm median particle diameter (Wieser 1959). Body size of the meiofauna tends to decrease as grain size, and consequently pore size, decreases (Swedmark 1964). The results of this study show that the average sizes of copepods and ostracods were positively correlated with grain size (Fig. 7). Witte & Zijlstra (1984) also found this positive correlation for copepods. The fact that the size of some major taxa is negatively correlated with the shear strength can be due to the fact that the higher the physical alteration of the sediment (less shear strength), the higher the size the fauna that will bear the mechanical impact of that alteration.

In conclusion, this study has shown that the intertidal meiofauna inhabiting exposed sandy beaches of southern Chile is closely related to beach characteristics. While the highest density and biomass values per m^2 were found at the reflective side of the beach spectrum sampled, density and biomass per linear meter of beach were higher at the dissipative beach. Thus, these results do not agree at all with the prediction of McLachlan & Turner (1994); i.e., higher abundance of meiofauna at intermediate sandy beaches. If this trend still holds along a complete spectrum of beach types along the coast of southern Chile or elsewhere remains an open question.

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